On the Maxillary Glands and some other Features in the Internal Anatomy of Squilla.

By

W. N. F. Woodland,
The Muir Central College, Allahabad, India
(late of University College, London).

With Plate 28 and 9 Text-figures.

CONTENTS.

I. THE MAXILLARY GLANDS.

Preliminary Comments.

THE following description of the maxillary gland of Squilla was intended to form but a small part of a monograph dealing with the anatomy in general of this aberrant Crustacean, but in consequence of my appointment to the Chair of Zoology at the Muir Central College, Allahabad, this project of a monograph has had to be abandoned. Since the description, so far as it goes, is fairly complete and intelligible, I have thought it worth while to publish it, together with a few notes on other parts of the anatomy of Squilla.

As is well known, the general text-book statement that antennal glands are characteristic of adult Malacostraca in the same way that maxillary glands are of "Entomostraca" now admits of many exceptions, since maxillary glands have been found in a number of undoubted Malacostracan genera. Maxillary glands have been described in adult forms of Leptostraca (Nebalia, Claus [7]), of Syncarida (Anaspides [3]), of Tanaidacea (Apseudes, Claus [8]), of Isopoda (Bopyrus, Gyge, Porcellio, Ligia, Asellus, Rogenhofer [21]), and of Stomatopoda (Squilla, Kowalevsky [14]). Since the researches of Grobben (10), Marchal (17), Kingsley (13), Waite (23), and others have demonstrated the high degree of complexity attained by the antennal glands in the higher and larger Malacostraca, it is perhaps surprising that the condition of the glands in the large-sized and, in many respects, highly developed and aberrant Squillidæ should not hitherto have attracted the attention of zoologists, especially in view of the statement of Kowalevsky (14) that the glands are maxillary and not antennal. However, apart from the rough figure by Claus (4, Taf. iv, fig. 8) of the maxillary glands in a late Stomatopod larva, the bald statement of Kowalevsky that they exist in the adult Squilla, and the preliminary description of these glands which I read (25) before Section D at the 1911 meeting of the British Association for the Advancement of Science (Portsmouth), nothing has been published on the subject.

As material for this inquiry, I employed adult specimens of Squilla desmarestii (Risso) and Erichthus larvæ of Lysiosquilla eusebia (2 mm. in length, and comparable with the figures 191 A and B shown in Calman [3]), obtained from Naples and fixed and preserved by the methods enumerated in the Appendix; also well-fixed Erichthus larvæ of an unknown species of Squilla, 12 mm. and 14 mm. in length respectively, preserved in the store-room at University College, London. Several complete series of transverse and longitudinal vertical sections were made of both adult and larval specimens, and the following description is based upon the careful study of these sections, assisted by dissections both of adult Squilla desmarestii and Squilla mantis and whole mounts of the smaller larvæ.

Before proceeding further I wish to offer my sincere thanks to Dr. W. T. Calman for kindly seeing the MS. through the press, and to Miss E. M. Brown for the careful drawings which illustrate the paper.

The Maxillary Glands of the Adult Squilla Desmarestii.

Macroscopic Appearance.

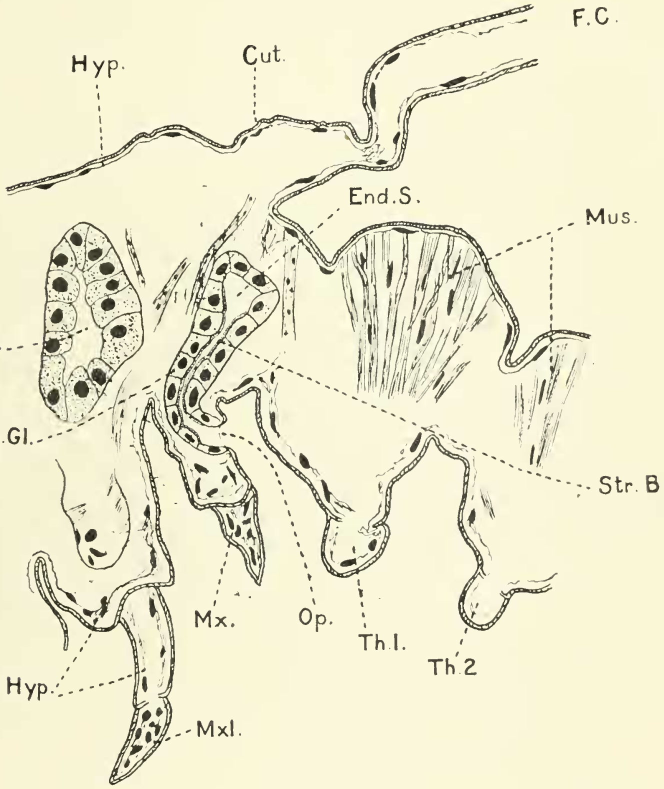
The paired maxillary glands lie at the hinder end of the "neck" of the animal, nearly on a level with the proximal joint and epipodite of the large subchelate second thoracic limb. Previous to dissection they may be seen through the transparent cuticle covering the sides of the neck as large yellowish masses, provided that the anterior thoracic limbs be pulled outwards from their forwardly directed position under the sides of the carapace. On removal of the dorsal carapace the paired glands are found to lie just under the hypodermis. Superficially, the glands closely resemble a pair of adductor muscles (the vertically descending gland-ducts simulating tendons) connected with the mandibles (Pl. 28, fig. 1), and it seems probable that they have been identified as such by previous observers, since otherwise it is difficult to understand how such conspicuous structures could escape attention. Viewed from the dorsal aspect, each of the two glands is seen to be a pear-shaped, compact yellowish mass, which tapers ventrally into a thin stalk, the stalks of the two glands converging towards the median line and disappearing one on each side of the large sub-œsophageal compound ganglion (*U. Th. G.*, Pl. 28, fig. 1). On closer inspection (Pl. 28, fig. 2) the thick upper portion of the pear-shaped gland is seen to be deeply grooved on its outer side to allow space for a large body-muscle which happens to traverse the body-cavity in the proximity of the gland. Although the gland is, in parts, closely wrapped round the muscle, yet there is, of course, no organic connection between the two structures In fig. 2 (Pl. 28) the duct of the gland is seen to enter the base of the maxilla (the second maxilla), and, after dilating slightly to form a bladder, to open on the extremity of the small papilla already described by Calman (**3**), who had previously suggested that the minute orifice present might prove to be that of the maxillary gland. In fig. 2 (Pl. 28) are also shown the numerous minute flask-shaped multicellular glands which are to be found scattered in many other regions under the hypodermis. These glands are connected with the setæ borne on the cuticle, and have been previously figured and described (under the general name of "drüsenzellen," and often incorrectly stated to be unicellular glands) by Claus (**5**), Jurich (**12**) and others. A drawing of a section through one of these glands (showing the gland lumen) is shown in Text-fig. 8. Fig. 2 (Pl. 28) represents the isolated maxilla and the attached gland as seen in spirit under the dissecting microscope; when in balsam the numerous seta glands are usually almost invisible, since staining reagents rarely penetrate sufficiently in order to render them conspicuous. The minute papilla with its gland opening is situated on the convex side of the maxilla, i. e. away from the mouth. The gland itself is, as we shall see, closely invested with squamous epithelium, and in size is about 4 mm. long, excluding the duct and the bladder, and about 2·5 mm. in maximum width.

General Histology.

The general position in the body and histological construction of the gland may be gathered from a perusal of fig. 3

(Pl. 28), which represents the gland and other organs in a transverse section of the left side of this region of the body. Most of the hæmocœle in this region is seen to be occupied

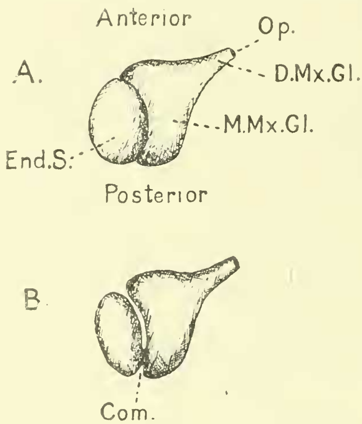
TEXT-FIG. 1.



Maxillary gland in a sagittal section of the larva of Lysiosquilla eusebia, 2 mm. long. *End. S.* Future end-sac. *M. Mx. Gl.* Future kidney. *Op.* Opening of gland duct. *Str. B.* Striated border of gland-cells of kidney portion (absent in cells of end-sac). (× 384.) For other reference letters see p. 429.

by large oblique longitudinal and transverse muscle bands and the maxillary glands. The parts of the gland shown in this figure, however, do not all occur in any one of my thin sections, but extend through several—the figure may be described as plano-stereoscopic. The mass of the gland lies behind the opening of the duct on the maxilla, seventeen sections (each 10 μ thick), intervening between that exhibiting this opening and that showing the end-sac in the upper part of the gland. In one respect only is the part of fig. 3 (Pl. 28) representing the gland obviously conventional, and that is the scale of magnification of the details showing the general structure of the gland mass—the cell-layers and ducts are

Text-fig. 2.

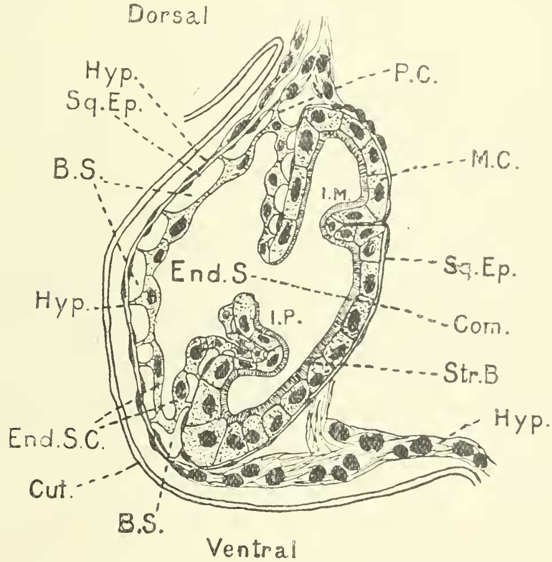


A. Reconstructed figure of the external appearance of the gland viewed dorsally in a larva 12 mm. long. In B the end-sac is supposed to be dragged apart from the kidney in order to show the postero-dorsal situation of the connection between the two. *End. S.* End-sac. *M. Mx. Gl.* Kidney portion of gland. *D. Mx. Gl.* Duct of gland. *Op.* Opening of duct. *Com.* Tubular connection between end-sac and kidney. (× 100.)

exhibited as large and few in number, whereas in actuality they are so small and numerous as to be undepictable in a drawing of this magnification. This excusable convention has the advantage of showing at a glance the general architecture of the entire organ.

The essential structure of the gland will be best comprehended by a preliminary reference to the early stages of its development. In the earliest stage of development found in our material the entire gland consists of a simple deep pocket, somewhat dilated at its blind extremity, which has apparently been formed by an involution of the hypodermis, i.e. the ectodern (Text-fig. 1). At a later stage the gland consists of two wide sacs which only communicate with each other by a narrow tube—the distal or "end-sac" and the

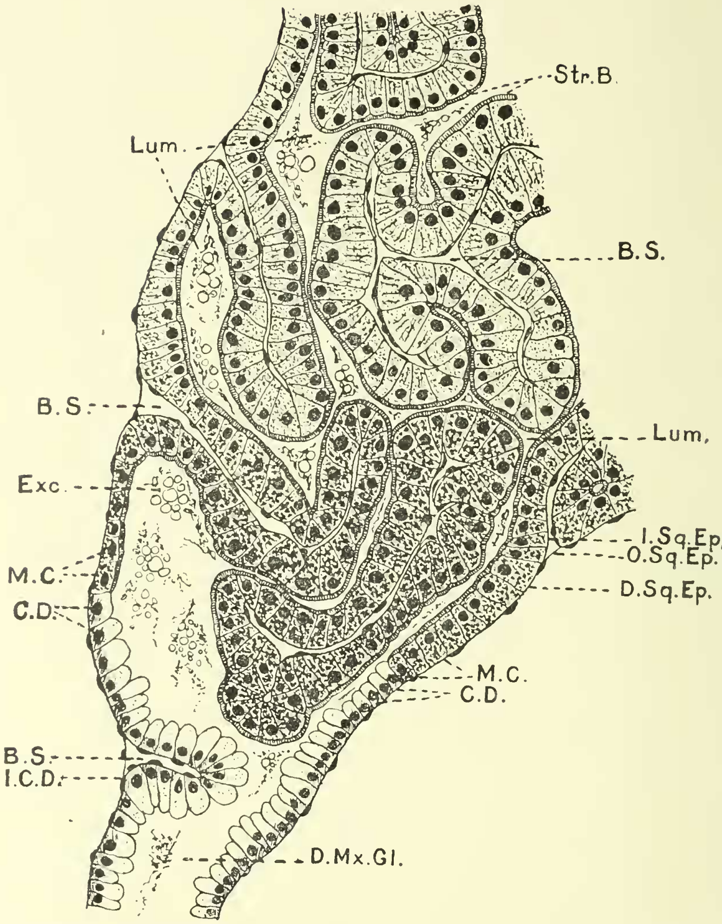
Text-fig. 3.



Transverse section across the end-sac and terminal part of the kidney of the gland (in a transverse section of a 14 mm. larva) showing the connection (*Com.*) between the two. *Cut.* Cuticle. *Hyp.* Hypodermis. *Sq. Ep.* Squamous epithelium underlying hypodermis. *End. S. C.* End-sac cells. *B. S.* Blood-sinus (contained blood not shown). *P. C.* Protoplasmic processes from end-sac cells extending across blood-space to squamous epithelium. *I. M.* Invagination of kidney wall in process of formation. *I. P.* Similar invagination of septum separating end-sac from kidney. (× 384.) For other reference letters see p. 429.

proximal sac or gland proper or kidney, as I shall term it in future, which opens to the exterior viâ the duct (Text-figs. 2 and 3). During subsequent development each of these divisions, but especially the kidney, enlarges greatly, and

Text-fig. 4.



Structure and histology of kidney and proximal duct portion of the gland in the adult Squilla. *Lum.* Lumen of gland containing excretory matter (*Exc.*). *B. S.* Blood-sinus (morphologically external to gland). *O. Sq. Ep.* Outer layer of squamous epithelium forming external wall of blood-sinus. *I. Sq. Ep.* Inner layer of squamous epithelium (forming inner wall of blood-sinus). *D. Sq. Ep.* The double layer of squamous epithelium. *I. C. D.* Invagination of duct-cells. Note absolute distinction between duct (*C. D.*) and kidney cells (*M. C.*) with striated border (*Str. B.*)—intermediate types do not exist. (× 296.)

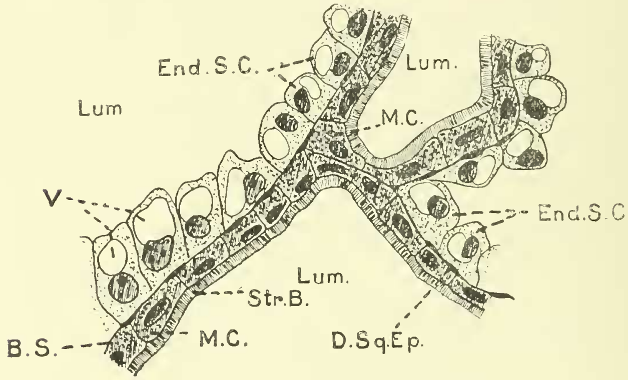
simultaneously their lumina become invaded by numerous invaginations of their walls (two incipient invaginations are shown in Text-fig. 3). These invaginations are formed at all points of the walls of the enlarged kidney and end-sac and become so long, branched and closely compacted internally in the former that the originally spacious lumen is reduced in all parts to thin cracks lying between adjacent cell-layers (Text-fig. 4). The entire exterior of the gland is invested with two layers of squamous epithelium, between which lies a division of the hæmocœle. The inner layer (*I. Sq. Ep.*, Text-fig. 4) only is closely applied to the surface of the entire gland, and becomes involved in all the invaginations just referred to. Careful inspection of well-stained sections shows (Text-fig. 4), as might be inferred from the development of the gland just outlined, that the mass of the gland exhibits two kinds of spaces : (i) Spaces hæmocœlic in nature, and therefore morphologically outside the gland, lined by the squamous epithelium, which originally covered the gland surface and which subsequently followed the invaginations of the gland wall ; and (ii) spaces devoid of a squamous epithelium, being solely bordered by the gland-cells, and representing all that is left of the originally wide lumen of the gland. Thus, it will be seen that the narrow blood-space surrounding the gland penetrates by means of the invaginations described into the innermost parts of the mass of the organ, and in every part is only separated from the lumen of the gland by a thin squamous epithelium and the single layer of gland-cells which purify the blood. The squamous epithelium forming the outer wall (*O. Sq. Ep.*) of the hæmocœle, and lying wholly on the periphery of the gland, lies for the most part in close contact with the inner squamous layer (*I. Sq. Ep.*), where this is situated at the periphery, and in my sections can only be distinguished from it at those points where the inner layer becomes invaginated to line the involutions of the gland wall, and so necessarily becomes separated (Text-fig. 4).

In longitudinal sections of the gland and duct (Pl. 28, fig. 3), the three regions characteristic of Crustacean antennal and maxillary glands can be distinguished : (*a*) The region of the end-sac, (*b*) the region of the kidney, and (*c*) the region of the duct.

Histology of the End-sac.

The region of the end-sac is distinguishable from the region of the gland proper by its relatively small size as compared with the kidney (though early in development they are equal

Text-fig. 5.



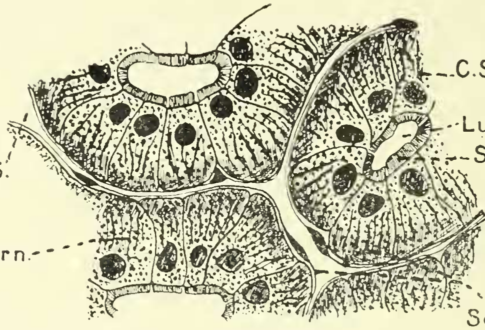
Cells of end-sac (*End. S. C.*) showing vacuoles (*V.*) and slightly granulated cells of kidney (*M. C.*) next end-sac (from longitudinal vertical section of adult Squilla). *B. S.* Very narrow blood-sinus. (× 810.) For other reference letters see p. 429.

in size), by its spacious lumen (the invaginations of the end-sac wall being few in number and simple in character) and by the character of the cells. The position of the narrow communication between the lumen of the end-sac and the kidney is very difficult to detect, since the opening is apparently not made evident by the presence of a couple or more of large "trichterzellen," such as those described by Allen (**1**) in the maxillary gland of the larva of Palæmonetes and by Vejdovský (**22**) in the antennal gland of Gammarus, and it is thus almost impossible to distinguish this narrow channel from the numerous other narrow channels penetrating the entire mass of the gland. If Text-fig. 3 be referred to, it will be seen that in the early stage of development figured, the septum (i. e. the apposed walls) separating the end-sac from the kidney is giving rise to an invagination in the same way as the other parts of the gland-wall, and hence the boundary between these two parts of the gland becomes very sinuous in the fully formed organ (Pl. 28, fig. 3), though easily distinguishable on account of the characteristic features of the end-sac cells. The end-sac as a whole is situated on the upper and slightly posterior and external lateral aspect of the fully formed gland, i. e. it retains the position in which it arose. The constituent cells of the end-sac of the fully formed gland (Text-fig. 5) are somewhat irregular in outline and consist of faintly granular cytoplasm, which is difficult to stain, and large nuclei. In close apposition to the nucleus of each cell is a large and very characteristic vacuole (*V*), usually much larger than the nucleus. These cells of the end-sac differ markedly from those of the gland proper, and the two kinds of cells are quite distinct—there are no cells transitional in character. The cells of the fully formed end-sac also differ greatly from those of the larval end-sac, as will be seen below. The blood-sinus, which extends into the septum separating the end-sac from the gland proper, is so attenuated in the gland of the adult as to be only recognisable in position by the nuclei of the two opposed layers of squamous epithelium composing its walls.

Histology of the Kidney or Gland Proper.

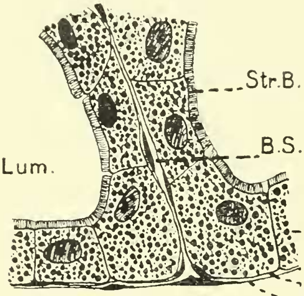
As already stated, in the region of the kidney, the wide lumen of the original sac is reduced to slit-like spaces situated between the crowded invaginations of the wall already described (Text-fig. 4). These thin spaces representing the gland lumen can always be distinguished from the equally thin extensions of the external hæmocœle by the facts that (A) the excretory matter contained in the lumen is largely in the form of spherical bubble-like masses (the blood, on the other hand, appearing as a fine sediment or homogeneous film), and (B) that they are lined, not by squamous epithelium, but by the excretory cells, the border of which, situated next the lumen, is characteristically striped. The

Text-fig. 6.



Cells of middle portion of kidney showing least amount of granulation, also striated border (*Str. B.*) and striations in cytoplasm (*C. Str.*). Blood-sinus (*B. S.*) relatively spacious. (× 810.)

Text-fig. 7.



Cells of kidney nearest duct showing greater granulation (*Grn.*). (× 810.) For other reference letters see p. 429.

cells composing the kidney vary slightly in character according to their position, those situated towards the end-sac, i. e. in the dorsal region, being far less granular and somewhat more columnar in form than the cells situated nearer the gland-duct. The more dorsally situated cells (Text-fig. 6) are large and columnar in form. The cytoplasm contains numerous small granules, is somewhat denser in the region next the hæmococele, and shows a faint striation parallel with the cell length. The portion of the cytoplasm bordering the lumen is, as above stated, characteristically striped. The nuclei are always situated near the striated border, and are large, with conspicuous chromatin granules. These less granular columnar dorsal cells pass gradually into the more granular and often flatter cells found towards the duct end of the gland (Text-fig. 7). The ventral cells chiefly differ from the dorsal in that the granules contained in the cytoplasm are more numerous and are much larger and that there are no striations in the general cytoplasm. It should also be mentioned that the cells composing the part of the kidney actually in contact with the end-sac are flat and small (Text-fig. 5), and that these gradually merge into the columnar kidney-cells already described.

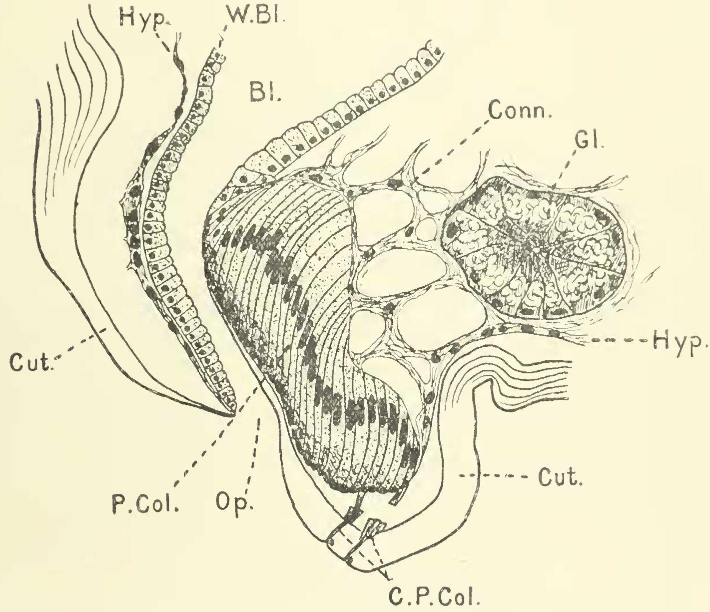
Histology of the Duct.

The duct region of the gland is distinguishable as a whole from the region of the kidney by the spacious lumen (a few wall invaginations only being present in the upper part of the duct) and by the character of the cells composing its wall. The character of the cells of the duct, indeed, enables this region to be distinguished with the greatest precision from the adjoining region of the gland proper, since, as can be seen in Text-fig. 4, there exist no cells intermediate in character between those composing the duct, on the one hand, and those composing the kidney on the other. We saw that the region of the gland proper could be sharply distinguished by the same means from the region of the end-sac, the cells of the latter being quite distinct in character.

The duct region of the gland can (Pl. 28, fig. 3) be subdivided into three sub-regions: (1) The upper duct, (2) the bladder, and (3) the duct aperture to the exterior. In the subregion of the upper duct the lumen is wide, contains a large quantity of excretory products, and is only slightly invaded by a relatively few simple wall-involutions (Pl. 28, fig. 3). The character of the cells forming the duct wall is shown in Text-fig. 4. The cytoplasm is faintly stained on the side situated next the lumen, but denser in appearance next the hæmocœle and is throughout faintly granular. The nuclei are large and spherical. In shape the cells are very irregular, and are quite devoid of the conspicuous striated border so characteristic of the cells of the gland proper. The nuclei, like those of the gland-cells, are situated at one end of the cell, but unlike those of the kidney, are situated next the hæmocœle and not next the lumen. Text-fig. 4 shows well the respective characters of the duct- and gland-cells and the abrupt transition from the one type to the other. Judging from the character of the cells of the duct, it seems probable that they take little or no share in the process of excretion. In the sub-region of the bladder the lumen is more spacious than in any other part of the gland and invaginations of the wall are quite absent. The cells of the walls are short, columnar or cubical in form (Text-fig. 8), and the cytoplasm is uniformly pale and faintly granular; there is no polar differentiation as in the cells of the upper duct. The nuclei are situated at the ends of the cells remote from the lumen. It is perhaps important to notice that the walls of the bladder near the external opening (Text-fig. 8) are devoid of the double layer of investing squamous epithelium found on the exterior of all other parts of the gland—a fact possibly of significance in connection with the question as to the germ-layer origin of the gland to be discussed later.

The bladder rapidly becomes narrow at its lower end to open to the exterior (Text-fig. 8). A notable feature of this external opening is the modification of the cells lining the inner and posterior side of the duct. As will be seen from fig. 3 (Pl. 28) and Text-fig. 8, the cells in the position stated become enormously elongated in a direction approximately parallel with the length of the duct to form a conspicuous clump of columnar cells continuous at the upper end with the cells of the bladder-wall and at the lower end with the cells of the hypodermis (the hypodermis has shrunk away from the cuticle all round the opening of the duct to the exterior). This clump of cells thus does not appear to form an ordinary sphincter muscle, since the muscle-fibres are not disposed

Text-fig. 8.



Opening of the gland. *Bl.* Lower portion of bladder. *Op.* Opening of duct. *P. Col.* Patch of columnar epithelium at duct opening, the lower cells of which are, in life, connected (*C. P. Col.*) with the two curious plug-like bodies situated in the cuticle (*Cut.*). *Gl.* Transverse section across one of the numerous small multicellular seta glands (drüsenzellen). The hypodermis has shrunk away from the cuticle. (× 384). For other reference letters see p. 429.

circularly round the narrow duct and they are only developed in the inner wall. If this clump of cells be examined carefully it is seen that the outer ends of most of these cells (containing denser cytoplasm) are in close contact with a thick strip of cuticle which extends up the inner wall of the duct and nowhere else, and that those cells situated at the extreme end of this duct opening (which have presumably shrunk away from the thick cuticle) are also connected with the cuticle by protoplasmic processes (nearly a dozen in number, though only about six are shown in the drawing) developed from their outer ends, which converge towards and become inserted into two curious plug-like bodies firmly imbedded in the cuticle (*C. P. Col.*, Text-fig. 8). These two plug-like bodies are not found in any other part of the body, and doubtless possess some special retentive function in connection with the cell-clump here developed. At their inner ends the cells composing the clump are ill-defined, and appear to merge into the numerous connective-tissue strands (*Conn.*, Text-fig. 8) occupying the cavity of the maxilla in this region. It is possible that the cells of the clump represent smooth muscle-fibres (they are not striped transversely), which on contraction serve to block up the external aperture of the gland. It is certain that the clump is not glandular, developed for the purpose of secreting the extra thick cuticle in this region, since the ordinary hypodermis is not specially developed elsewhere to produce this result, and it is difficult to suppose that the clump possesses a sensory function, though the pigment (?) spots associated with the two "plugs" at first suggest this.

Some Stages in the Development of the Maxillary Gland.

The Gland of the 2 mm. Larva of Lysiosquilla eusebia.—In some Erichthus larvæ of Lysiosquilla eusebia, 2 mm. in total length, comparable with the developmental stage figured, after Claus, by Calman (**3**) in his fig. 191A (only the second thoracic limb in my specimens has not yet become enlarged), and, with the exception of the "metanauplius" stage of Lister (**16**), representing the youngest larval form of Squilla yet known, the maxillary gland is of the simple form represented in Text-fig. 1. The gland at this early stage of development solely consists of a simple, deep, pocket-like ingrowth opening at the base of the maxilla on its posterior outer side and possessing a blind extremity which is somewhat dilated. This blind extremity lies just under the junction of the free carapace (*F. C.*) with the body and just behind the diverticulum of the gut (*G. D.*) which will subsequently form the "liver." Text-fig. 1 is plano-stereoscopic (combines in one plane parts which are only to be found in separate sections and which would only be visible collectively under the microscope if the section were of sufficient thickness to contain them all), and represents the gland as seen in sagittal sections of the larva. In a series of transverse sections of the larva, the gland was only included in eight successive sections, each 10 μ thick, and appeared as a small tube cut transversely owing to the gland slanting posteriorly in position. The gland is, in all probability, functional at this early stage of development, since, with the exception of those situated at the extreme end of the diverticulum and at the external opening, all the cells (in the middle part of the gland labelled *M. Mx. Gl.*) possess the striated border so characteristic of the excretory cells of the gland proper in the fully formed organ and contain granules in the cytoplasm. The fact (perhaps I should say probability, since the sections do not afford quite conclusive evidence) that the extreme cells of the terminal dilatation do not possess a striated border certainly favours the conclusion that this region becomes the end-sac of the fully formed gland. If this last statement be true (and there is but little doubt about it), then, in view of the obvious continuity of the wall of the gland diverticulum with the hypodermis at the external opening (see Text-figs. 1 and 8) and the absence of mesenchymatous cells in the vicinity of the gland (the gland is apparently not invested by squamous epithelium at this stage), it seems extremely probable that the whole of the diverticulum (and therefore the whole of the fully formed gland, end-sac and all) is the product of an involution of the hypodermis, i.e. ectoderm. The probability of this conjecture is discussed below.

The Gland in a 12 mm. Larva, Squilla sp.—The stage of development of the maxillary gland in this larva is indicated in Text-fig. 2, A and B, which represents a reconstructed stereoscopic view of the gland based on a series of drawings, drawn to scale, taken from the serial sections. In this figure the gland is viewed from the dorsal aspect (cf. Pl. 28, fig. 1, showing the adult gland). In A the three parts of the gland, which are now easily distinguishable, are shown in their correct relative positions. The end-sac (*End S.*) is shown to lie on the postero-dorsal aspect of, and in close apposition with, the kidney (*M. Mx. Gl.*), and the latter is, of course, continuous with the vertically descending duct (*D. Mx. Gl.*), the terminal part of which is not yet dilated to form a bladder. In B the end-sac is supposed to have been pulled apart from the kidney in order to show the posterior position of the narrow canal (*Com.*) putting the two parts into communication.

The Gland in a 14 mm. Larva, Squilla sp.—Though the Erichthus larva of this size is not much larger than that of the preceding stage, and the maxillary glands of both stages are practically identical, yet the gland of the older larva differs in one small though important feature from that of the younger. In a transverse section of the gland at this stage of development (Text-fig. 3) passing through the narrow communication (*Com.*) between the end-sac and the kidney, the cavities and walls of these two regions are well shown. The cells composing the wall of the cavity representing the kidney (*Mc.*) are very similar to those found in the gland of the adult Squilla. They are regular in outline and stain deeply; the cytoplasm is granular, and there is a well-defined striated border present (*Str. B.*). The quite different cells composing the wall of the end-sac (*End. S. C.*) are, on the other hand, very dissimilar to those of the fully formed gland. As shown in the figure the faintly granular cytoplasm is drawn out at irregular intervals into tent-like projections (*P. C.*), which stretch across the intervening space (hæmocœle) to the layer of squamous epithelium surrounding the whole gland. These projections are apparently found in connection with the end-sacs of most antennal and maxillary glands, since they are figured by Grobben (**10**), Claus (**6**), Vejdovský (**22**), and many other authors. Finally, it will be noticed that these end-sac cells contain none of the vacuoles so characteristic of the cells composing the fully formed end-sac.

As regards the squamous epithelial investment of the gland at this stage of development it will be remembered that in the adult Squilla the whole of the gland, excepting the lower part of the bladder, is enclosed in a double layer of squamous epithelium, the two layers enclosing a blood-space. On the other hand, in the early stage of development of the gland depicted in Text-fig. 1 no epithelial investment whatever can be observed. Text-fig. 3 shows what may perhaps be regarded as an intermediate condition. As will be seen, the gland at this stage lies in close contact with the side of the body, and is only separated from the hypodermis by a (apparently) single layer of squamous epithelium (*Sq. Ep.*), which is also to be found on the inner side of the gland, and penetrates between the closely apposed walls of the end-sac and the gland proper. This single layer of squamous epithelium also penetrates into the invaginations of the wall, the presence of which distinguishes the gland of the 14 mm. larva from that of the 12 mm. In this 14 mm. larva, therefore, we can observe the commencement of the formation of those involutions of the wall of the gland proper (two are shown in Text-fig. 3—*I.M.* and *I.P.*), which ultimately so invade the cavity of this region as to reduce it to the winding system of narrow cracks already described as characteristic of the fully formed organ. Since the single layer of investing squamous epithelium is drawn into each of these involutions of the wall, it must therefore represent the inner layer of the two layers characteristic of the adult condition. The outer layer of squamous cells of the adult gland is possibly produced later by the splitting (delamination) of the inner (I admit that the only evidence I have for this suggestion is the occasional appearance, in sections, of a double condition to be found over small areas of the single squamous layer.) The duct to the exterior is composed of cells similar to those of the gland proper, save that they lack the striated border. There is as yet no dilatation to form a bladder.

Remarks on the Maxillary Gland of Squilla compared with the Excretory Leg Glands of other Crustacea and Arthropoda.

If we compare the maxillary glands of Squilla with those of the Isopoda (described by Rogenhofer [21]) it is at once evident that the former greatly exceed the latter in complexity of structure, and in fact the maxillary glands of the adult Bopyrus, Porcellio, and even Ligia are almost exactly comparable, both as regards general form and histology, with the early stage of development of the maxillary gland found in the 12 mm. larva of Squilla. In Asellus aquaticus, on the other hand, the kidney region of the gland has, according to Rogenhofer, become much lengthened and convoluted and therefore more similar to the maxillary gland of Branchipus (Claus [6]) or the antennal glands of Gammarus (Vejdovský [22] and Mysis (Grobben [10]). In connection with the antennal and maxillary glands of Malacostraca generally it appears that the kidney part of the gland is able to undergo complication in two different ways: (1) It may either elongate and become greatly convoluted (Asellus, Gammarus, Mysis), or (2) it may swell and its wall become invaginated by inward extensions of the external hæmocœle. As examples of the latter method may be mentioned the maxillary gland of Squilla and the antennal glands of Cancer (Pearson [18]), Homarus (Waite [23]), Palæmonetes (Allen [1]), etc. I should like here to record my suspicion that many descriptions (e.g. Waite's description of the antennal gland of Homarus ([23]) and Weldon's description of the kidney region of certain other Decapods [24]) of the structure of the kidney region of the antennal gland in different genera of Malacostraca commit the error of describing as an elongated convoluted duct what should be described as the extensive invagination of a swollen sac. In both cases sections would reveal tubular structures cut across, and it is only by careful reconstruction and examination of the investing epithelia that the observer can be certain as to which type of structure his sections represent.

Concerning the comparative histology of the maxillary gland of Squilla, I must remark that in general it resembles that of the antennal and maxillary gland of other Crustacea, as reference to the works of Grobben, Rogenhofen, Allen, Vejdovský and others will show.

As regards the germ-layer origin of the antennal and maxillary glands in Crustacea, it is interesting to note the differences of opinion among authors on the subject. For instance, my figure of the youngest stage of development of the maxillary gland of Squilla closely resembles those of Ishikawa ([**11**], his fig. 92) and Grobben (**10**), representing the early development of the antennal glands of Atyephira and Cetochilus respectively, but whereas Ishikawa states that the young gland is ectodermal in origin, Grobben holds that it is mesodermal, arising as an invagination of the somatopleure. Reichenbach (**19**) held that the antennal glands of Astacus are purely ectodermal structures, and a number of later authors agree that at least the external part of the gland in the Crustacea is of ectodermal origin, e. g. Ishikawa (**11**) believes that the entire gland of Atyephira is ectodermal, whilst Lebedinsky (**15**), Boutchinsky (**2**) and Waite (**23**) state that the duct and kidney are ectodermal, the end-sac being mesodermal. On the other hand, Grobben (**10**), Kingsley (**13**) and Robinson (**20**) consider the whole gland to be a mesodermal product, but Grobben's statement concerning the somatopleuric invagination is certainly difficult to believe, since a cœlomoduct is formed as an outpushing, not an ingrowth, and Robinson's figures of the first rudiments of the antennal gland in Nebalia show that the initial clump of cells may just as well be considered ectodermal as mesodermal. It must be concluded, I think, that the evidence for the ectodermal origin of the duct and kidney of the gland is preponderant. Concerning the origin of the end-sac, the evidence is not so one-sided. The statements of Waite, confirming those of Lebedinsky and Boutchinsky, are quite definite as to the origin of the end-sac in a distinct mass of mesoderm cells, and the secondary junction of the end-sac with the ectodermal kidney and duct. On the other hand, Grobben figures the end-sac cells as forming the upper extremity of the simple invagination in the early development of the gland, just as I have figured these same cells in my drawing of the youngest stage of the Squilla gland—there is no separate origin of the end-sac here—and Boutchinsky merely asserts that the deep end of the ectodermal invagination becomes surrounded by mesoderm cells—a statement which may have resulted from a mistaken conception of the origin of the "mesoderm" cells. Further, Waite's supplementary argument for the separate origin of the end-sac based upon the entirely distinct character of the cells of the end-sac as compared with those of the kidney counts for little; my description of the differences of the kidney and duct-cells and their abrupt distinctness (no transitional kinds of cell existing) in the gland of Squilla might equally well be employed to suggest that the kidney and duct regions are of separate origin. In view, then, of the scanty and conflicting evidence on the subject, we are not in a position to draw conclusions respecting the ectodermal or mesodermal origin of the end-sac, still less to discuss the homologies either of the various parts of the antennal and maxillary glands or of the glands as a whole. Future inquiry can alone decide whether or not these Crustacean leg-glands (rudiments of which, it must be remembered, have been found in connection with the maxillipedes [15] and other thoracic limbs in addition to the second antenna and second maxilla) are to be compared with the ectodermal crural glands rather than with the mesodermal excretory organs of Peripatus as heretofore.

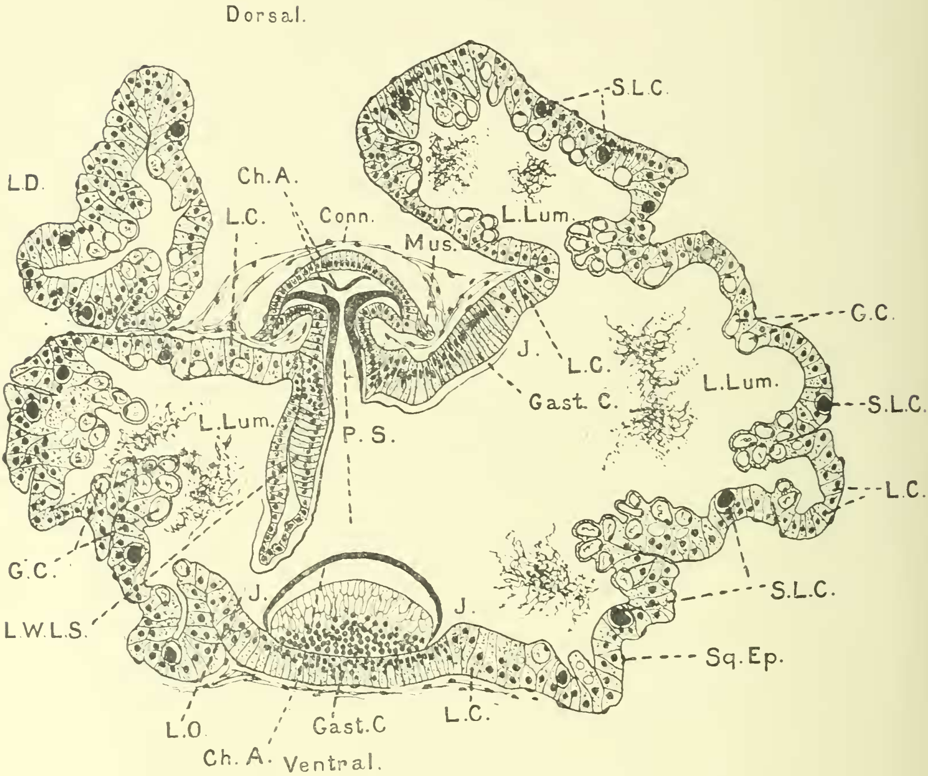
II. Notes on some other Features of the Internal Anatomy of Squilla.

The Communications between the Pyloric Digestive Gland ("Liver") and the Gut.

Johannes Müller (**29**) in 1830 made the statement that the so-called "liver" possessed numerous pairs of segmentally arranged openings into the alimentary tract, and later authors (e.g. Duvernoy, 1836 [**26**], Milne Edwards, 1859 [**27**], Gerstaecker, in Bronn's 'Thierreich,' 1889 [**31**] and others) have either accepted this statement on Müller's authority or have supposed that their reinvestigations have confirmed Müller. However, in 1901 Orlandi (**30**) to a large extent corrected this erroneous idea, and stated that the two halves of the "liver" solely opened into the gut by a single median opening into the dorsal side of the pyloric part of the stomach, and this statement has appeared in most recent English text-books, e.g. in Calman's "Crustacea" in Lankester's 'A Treatise on Zoology' and Sedgwick's 'Student's Text-book of Zoology.' It must be pointed out, however, that Fritz Müller (**28**) in 1863 clearly described and figured a single pair of "liver" ducts opening into the sides of the stomach in an Erichthus larva, and this fact would by itself lead us to suppose that the adult condition is similar to that of the larva.

A further correction concerning this much misinterpreted and, indeed, trivial point of fact has now to be made in the present paper. Orlandi was correct in stating that each half of the "liver" only possesses a single duct opening into the pyloric region, but quite wrong in stating that the two ducts unite together and open by a single mid-dorsal aperture. Examination of complete series of transverse and longitudinal sections through the adult Squilla desmarestii, Risso, shows that each duct opens independently into the side of the pylorus by a large triangle-shaped aperture (the apex of the isoceles triangle being anterior and the vertical base posterior), and so conforms to the arrangement found in most Crustacea. In front of these lateral openings of the pyloric gland into the stomach, the gland is produced into two blind diverticula which extend forwards as far as the base of the second

TEXT-FIG. 9.



Transverse section across pyloric region of stomach, showing the two lateral openings of the pyloric digestive gland (explained in the text). *L. O.* Anterior extremity of left opening of gland into stomach. *Gast. C.* Gastric cells. *L. Lum.* Lumen of digestive gland. *L. D.* Small dorsal diverticulum of gland. *P. S.* Cavity of pyloric stomach. *Ch. A.* Chitinous lining of stomach. *S. L. C.* Small cells. *G. C.* "Goblet" cells. (×173.) For other reference letters see p. 429.

thoracic limb. Each of these anterior diverticula is joined dorsally by a smaller diverticulum (*L. D.* in Text-fig. 9) at the level of the posterior end of the gland opening into the stomach.

Posteriorly to this opening the gland extends back on each side as a wide sac in close contact with the narrow intestine (which is thus effectively hidden from view), and gives off numerous lateral diverticula in its course. These diverticula are somewhat narrow proximally but dilate and branch distally; in the sixth abdominal segment they extend into the basal joints of the appendages borne on that somite, and they occupy the greater part of the cavity of the telson. Text-fig. 9 represents on its left side a section passing through the anterior extremity of the opening of the pyloric gland into the stomach, which is thus seen to be narrow and ventro-lateral; the right side of the same figure passes through the posterior extremity of the opening, which is thus evidently wide and lateral. Sections also show that the whole of the gland is enveloped in a large blood-sinus containing much blood.

The cells of the digestive glands are of several kinds, the most noticeable being the ordinary granular cells (*L. C.*), cells wedged in between the ordinary cells and containing large vacuoles (*G. C.*; these vacuoles burst into the gland cavity) and small cells with very large darkly-staining nuclei (*S. L. C.*).

The Rectal Glands.

The rectal glands are found in both sexes underlying the ramifications of the "liver" in the telson. They are two in number, are large, with spacious lumina, and open in the adult as in the larva (see Claus [**5**]), laterally at the posterior end of the rectum. In addition to these rectal glands there are present some small accessory tubules opening into the gut in the same region, which apparently bear some resemblance in structure to the urinary tubes of Amphipods.

The mesenteron is very long in Squilla and extends from the stomach to the region of the anus, where the cuticle of the proctodæum becomes inturned for only a short distance.

The Nauplius Eye.

The Nauplius eye persists in the adult Squilla, and can easily be seen under a low-power binocular as a small patch of black pigment lying towards the ventral side of the head between the bases of the paired stalked eyes. The pigmented eye apparently contains in the specimens examined either two or three ocelli (probably three, since this is the number found in most Crustacea), and is connected by a single slender nerve to the brain.

Appendix.

Methods of Preparation of Material.

The adult specimens of Squilla desmarestii were fixed for me at Naples in Hermann's fluid, in Zenker's fluid, in corrosive-acetic and in hot absolute alcohol. On receiving them I carefully decalcified certain specimens in a mixture of nitric acid (over 5 per cent.) in alcohol (the liquid constantly renewed) for three or four weeks. They were then embedded in hard (60° C.) wax and cut into sections 10 μ thick. Despite the thickness of the cuticle, complete series of transverse and longitudinal vertical sections were obtained of three entire animals. Complete series of transverse and longitudinal sections were also made of many larvæ of the sizes mentioned in the above description. All these sections were double-stained on the slide in Ehrlich's hæmatoxylin (twenty-four hours), followed by picro-indigo-carmine. (Add one part saturated solution of picric acid in 90° alcohol to two parts saturated solution of Grübler's indigo-carmine in 70 per cent. alcohol, and dilute this stain with equal bulk of 70 per cent. alcohol; for mode of using this stain see my paper on "Fish Gas Glands," 'Proc. Zool. Soc. Lond.,' 1911.) Sections of the Hermann's fluid material were found to be best preserved.

Literature relating to the Maxillary Gland.

1. Allen, E. J.—"Nephridia and Body-cavity of some Decapod Crustacea," 'Quart. Journ. Micr. Sci.,' vol. 34, 1892–93.

2. Boutchinsky.—'Mem. Soc. Nat. New-Russia,' T. xix (Part 2), 1895.

3. Calman, W. T.—The Fascicle on "Crustacea" in Lankester's 'Treatise on Zoology,' 1909.

4. Claus, C.—'Untersuchungen zur Erforschung der genealogischen Grundlage des Crustaceen-systems: ein Beitrag zur Descendenzlehre," Wien, 1876.

5. ——— "Die Kreifslaufsorgane und Blutbewegung der Stomatopoden," 'Arb. Zool. Inst. Univ. Wien,' Bd. v, 1883.

6. ——— "Untersuchungen über die Organisation und Entwickelung von Branchipus und Artemia, nebst vergleichenden Bemerkungen über andere Phyllopoden," 'Arb. Zool. Inst. Univ. Wien,' Bd. vi, 1886.

7. ——— "Ueber den Organismus der Nebaliden und die systematische Stellung der Leptostraken," 'Arb. Zool. Inst. Univ. Wien,' Bd. viii, 1889.

8. ——— "Ueber Apseudes Latreillii, Edw. und die Tanaiden," 'Arb. Zool. Inst. Univ. Wien,' Bd. ix, 1891.

9. Defner, A.—"Der Bau der Maxillardrüse bei Cirripedien," 'Arb. Zool. Inst. Univ. Wien,' Bd. xviii, 1910.

10. Grobben, C.—"Die Antennendrüse der Crustaceen," 'Arb. Zool. Inst. Univ. Wien,' Bd. iii, 1881.

11. Ishikawa, C.—"On the Development of a Freshwater Macrurous Crustacean, Atyephira compressa, De Haan," 'Quart. Journ. Micr. Sci.,' vol. 25, 1885.

12. Jurich, Bruno.—"Die Stomatopoden der deutschen Tiefsee-Expedition," 'Wissenschaft. Ergeb. Deutsch. Tiefsee-Expedition auf dem Dampfer "Valdivia," 1898–99,' Bd. vii, 1904.

13. Kingsley, J. S.—"The Development of Crangon vulgaris," (third paper), 'Bull. Essex Inst.,' vol. xxi, 1889.

14. Kowalevsky, A.—"Ein Beitrag zur Kenntnis der Exkretionsorgane," 'Biol. Centralblatt,' Bd. ix, 1890.

15. Lebedinsky, J.—'Mem. Soc. Nat. New-Russia,' t. xiv (Part 2), 1889.

16. Lister, J. J.—"Note on a (? Stomatopod) Metanauplius Larva," 'Quart. Journ. Micr. Sci.,' vol. 41, 1898.

17. Marchal, P.—"Recherches Anatomiques et Physiologiques sur l'Appareil Excréteur des Crustacés Décapodes," 'Arch. d. Zool. Exp. et Générale,' Paris, Ser. 2, T. x. 1892.

18. Pearson, J.—Memoir on Cancer in the Series of the Liverpool Marine Biological Committee, 1908.

19. Reichenbach, H.—"Die Embryonalanlage und erste Entwicklung des Flusskrebses," 'Zeit. f. wiss. Zool.,' Bd. xxix, 1877.

20. Robinson, M.—"On the Development of Nebalia," 'Quart. Journ. Micr. Sci.,' vol. 50. 1906.

21. Rogenhofer, A.—"Zur Kenntnis des Baues der Kieferdrüse bei Isopoden und des Grössenverhältnisses der Antennen- und Kieferdrüse bei Meeres- und Süsswasserkrustazeen," 'Arb. Zool. Inst. Univ. Wien,' Bd. xvii, 1908.

22. Vejdovský, F.—"Zur Morphologie der Antennen- und Schalendrüse bei Crustaceen," 'Zeit. f. wiss. Zool.,' Bd. lxix. 1901.

23. Waite, F. C.—"The Structure and Development of the Antennal Glands in Homarus americanus, Milne Edwards," 'Bull. Mus. Comp. Zool. Harv.,' vol. xxxv, 1899–1900.

24. Weldon. W. F. R.—"The Renal Organs of certain Decapod Crustacea," 'Quart. Journ. Micr. Sci.,' vol. 32, 1891.

25. Woodland, W. N. F.—"On the Renal Organs and some other Features of the Internal Anatomy of Squilla," 'Report (Section D) of Brit. Assoc. Advance. Sci.,' Portsmouth, 1911.

Literature relating to the Pyloric Digestive Glands ("Liver") of Squilla.

26. Duvernoy, G. L.—"Sur le Foie des Animaux sans Vertèbres en général et particulièrement sur celui de plusieurs Crustacés," 'Ann. Sci. Nat.,' ser. 2. t. vi, p. 243, pl. 15, Paris, 1836.

27. Milne Edwards, H.—'Leçons sur la Physiologie et l'Anatomie comparèe," t. v, Paris, 1859, pp. 557, 566.

28. Müller, F.—"Ein zweites Bruchstück aus der Entwickelungsgeschichte der Maulfüsser," 'Arch. f. Nat.,' Bd. xxix, pp. 1–6, pl. 1, 1863.

29. Müller, J.—'De Glandularum secernentium Structura.' Lipsiæ, 1830, p. 69.

30. Orlandi, S.—"Sulla Struttura dell' Intestino della Squilla mantis (Rond.)," 'Atti. Soc. Ligustica,' vol. xii, pp. 112–133, 2 plates, 1901.

31. Gerstaecker, A.—"Crustacea" in Bronn's 'Klassen und Ordnungen des Thierreichs,' Bd. v, Abth. 2, 2te Hälfte, pp. 705–707, 1889.

REFERENCE LETTERS OF FIGURES (PLATE AND TEXT).

A. 1. Antennula. *A.* 2. Antenna. *Bl.* Bladder. *B. S.* Blood-space (hæmocœle). *C.* Carapace. *C. D.* Duct-cells. *Ce. A.* Cephalic aorta. *Ch. A.* Chitinous armature of stomach. *Conn.* Connective-tissue strands. *C. P. Col.* Connections between columnar cells and "plugs" in cuticle. *C. Str.* Striations in cytoplasm of kidney-cells. *Cut.* Cuticle. *D. Mx. Gl.* Duct of maxillary gland. *Ds.* Dorsal surface of gland. *D. Sq. Ep.* Double layer of squamous epithelium. *E.* Eye. *End. S.* End-sac. *End. S. C.* End-sac cells. *Ep.* Epipodite. *Ep.* 2. Epipodite of second thoracic appendage. *Ex.* Scale-like exopodite of antenna. *Exc.* Excretion material. *F. C.* Free carapace. *Gast. C.* Gastric cells. *G. C.* Goblet-cells. *G. D.* Lateral diverticulum of duct. *Gl.* Glands ("drüsenzellen"). *Gr.* Groove on side of gland lodging body muscle. *Grn.* Granules. *H.M.* Hæmocœle. *Ht.* Heart. *Hyp.* Hypodermis. *I. C. D.* Invagination of duct-cells. *I. M.* Invagination of kidney wall. *I. P.* Invagination of partition wall separating end-sac and kidney. *I. Sq. Ep.* Inner layer of squamous epithelium. *J.* Junction of gastric and hepatic cells. *L.* Pyloric digestive gland ("liver"). *L. C.* "Liver" cells. *L. D.* "Liver" diverticulum. *L. Lum.* "Liver" lumen. *L. O.* "Liver" opening into stomach. *Lum.* Lumen—excretory. *L. W. L. S.* Apposition of "liver" and pyloric stomach on left side. *M. C.* Kidney-cells. *M. Mx. Gl.* Kidney portion of gland. *Mx.* Maxilla. *Mx. Gl.* Maxillary gland. *Mxl.* Maxillula. *Mus.* Muscles. *Mus. Lon.* Longitudinal muscles. *Mus. Tr.* Transverse muscles. *Nc.* Nerve cord. *Op.* Opening of maxillary gland on papilla. *O. Sq. P.* Outer layer of squamous epithelium. *P. C.* Protoplasmic processes from end-sac cells traversing blood-space. *P. Col.* Mass of columnar epithelium at opening of maxillary gland-duct. *P. S.* Pyloric portion of stomach. *R.* Rostrum. *S. L. C.* Small special "liver" cells (resembling oxyntic cells). *Str. B.* Striated border of kidney-cells. *Sp. Ep.* Squamous epithelium. *Th.* 1, *Th.* 2, *Th.* 3 . . . *Th.* 7. Thoracic appendages. *U. Th. G.* United ganglia supplying the mandibles and the first five thoracic segments and bearing the circum-œsophageal connectives anteriorly. *V.* Vacuole. *W. Bl.* Wall of bladder.

EXPLANATION OF PLATE 28,

Illustrating Mr. W. N. F. Woodland's paper, "On the Maxillary Glands and some other Features in the Internal Anatomy of Squilla."

[All figures of Squilla desmarestii, and all drawn by means of the camera lucida.]

Fig. 1.—Anterior end of Squilla, dissected to show the maxillary glands (*Mx. Gl.*) in sitû. The carapace has been cut away dorsally over a large area, and the underlying hypodermis, some large oblique and longitudinal body muscles, the anterior cæca of the liver, and part of the gut and cephalic aorta have been also removed. (× 3.)

Fig. 2.—The maxillary gland (*Mx. Gl.*) removed from the body with the second maxilla and viewed laterally. Its external aperture (*Op.*) on the papilla (situated on the outer or convex side of the limb), the bladder (*Bl.*) and the mass of the gland can be seen. Most of the muscles entering the limb have been removed, and two are represented in outline by dotted lines. *Gl.*, small gland-cells. (× 6.)

Fig. 3.—Transverse section across the left side of Squilla in the region of the maxillary gland. As mentioned in the text, the details of the gland structure are shown on an immensely magnified scale in order to make apparent the general construction of the gland; in reality the cell-layers of the gland are much smaller and much more numerous. *M. Mx. Gl.* General (kidney) mass of gland. *D. Mx. Gl.* Duct of maxillary gland. *Bl.* Bladder portion of gland. *Op.* Opening of maxillary gland on papilla. *P. Col.* "Plug" of columnar epithelium at opening of duct (see Text-fig. 8). (× 20.)